EFFEC'TOR PATTERN OF THE AUDIO-VISUAL TARGETING
REFLEX IN CATS

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Abstract. The development of the effector pattern of the uncondi-
tioned and instrumental conditioned audio-visual targeting reflex was
studied. EOG and EMG electrodes were implanted to analyze the move-
ments of the pinna, eye and head, when the animals localized a sound
source placed in different positions in space. When the acoustic stimu-
lus was repeated, the unconditioned targeting reflex was characterized
by a rapid intra- and intersessional habituation of the three motor
components. In the second part of the experiment the unconditioned
targeting reflex was reinforced by food to build up an instrumental
conditioned targeting reflex. It was shown, that under both experi-
mental conditions the targeting reflex began with the auricular compo-
nent, followed by the oculo-cephalic response. After conditioning the
latencies were decreased in comparison with the unconditioned reactions.
The shortest latencies and most stable responses were found in the
pinna muscles ipsilateral to the sound source. After conditioning the
resistance to extinction was increased for all three motor components,
but the pinna movement ipsilateral to the sound source was again the
component most resistant to extinction.

INTRODUCTION

Konorski (17) proposed in 1967 to call targeting reflex a motor
reaction directed to allow the animal the best perception of a given
stimulus. According to this terminology Santibáñez-H. (22) designated
as audio-visual targeting reflex the motor reactions elicited by an auditory stimulus which allows the animal to focus with the eyes the source of sound. Behavioral studies of Alvarado and Santibáñez-H. (1) have shown, that the unconditioned targeting reflex has three main components: auricular, oculo-cephalic and postural reactions. Different stages of development of the targeting reflex could be observed, such as formation, consolidation and inhibition of the reflex pattern.

The unconditioned targeting reaction presents a very rapid intra-session inhibition. This reaction is not suitable for studying problems such as the role of the ear movements where the reflex must be kept up for a long time. Aneiro-Riba and Santibáñez-H. (cit in 22) obtained a long lasting reflex by transforming the unconditioned into an instrumental reflex.

The present work was carried out in order to analyse the sequence of the motor components in the unconditioned and conditioned audio-visual targeting reflex, as well as in the process of inhibition of their effector patterns during extinction.

METHODS

The experiments were performed on 5 cats. The animals were naive adults weighing between 2.5 and 3.5 kg. The movements of the eyes, the ears and the head in an unconditioned and an instrumental conditioned targeting reflex situation were recorded.

Surgical procedure. The animals were operated under Pentobarbital anaesthesia (38 mg/kg) in aseptic conditions. After trepanation of the skull, miniature stainless steel electrooculographic electrodes were implanted in the lateral border of the right superior orbital bone in a manner that allowed the recording of the horizontal eye movements. For miographic recording of ear and head movements pairs of platinum-iridium electrodes \( (\Phi = 1 \text{ mm}) \) were implanted in the right and left levator auris longus muscle that pulls the pinna dorsocaudally and in the deeper dorsal neck muscles which are involved in the horizontal movements of the head. Fine spirals \( (\Phi = 0.5 \text{ mm}) \) of stainless steel wire \( (\Phi = 0.1 \text{ mm}) \) isolated by silicone rubber were led from the electrodes to a plug socket mounted on the vertex to minimize the restriction of ear and head movements.

Training procedure. The training was carried out in a situation similar to the one described elsewhere (26, 27). Four loudspeakers were placed in the upper corners of a cage of 1 m \( \times \) 1 m \( \times \) 0.8 m in frontal-right, frontal-left, posterior-right, posterior-left positions in relation to
the position of the head of the animal at the stimulus onset, when the animal assumed a central position in the cage with its head facing the midsection of the frontal wall.

First of all, the motor components of the unconditioned targeting reflex were studied in five sessions until habituation was achieved in each session. For this purpose the animals were stimulated by a repeated tone ($f = 1.6$ kHz, $i = 75$ dB, $\Delta t = 0.5$ s) delivered through a loudspeaker. After habituation the acoustic parameters were irregularly changed in order to elicit further targeting responses.

Because of rapid habituation, for further studies we established an instrumental conditioned targeting reaction. Each time the animal looked at the activated loudspeaker, it was rewarded with a piece of meat given through a carousel feeder. The response was considered correct, if at the first presentation of the above mentioned standard tone, the animal targeted the activated loudspeaker and not another one. In each session the loudspeakers were activated randomly. When the animals had reached at least 80% correct responses the extinction of the conditioned targeting reflex was introduced.

Recording and data analysis. The EOG and EMG data were registered on a conventional polygraph recorder at a speed of 100 mm/s. The latencies of the motor components were measured and mean values and variances were calculated. The nonparametric Walsh-test was used for the statistical analysis.

RESULTS

Sequence of motor components in the targeting reflex. Unconditioned targeting reflexes. The latencies of the auricular, ocular and cephalic motor reactions integrating the targeting responses elicited by a neutral auditory stimulus indicate that these reactions occur in a temporal sequence (Table I). The auricular reaction with a mean value of 78 ms
has a significantly shorter latency than the ocular and cephalic ones. However, the differences between these last two reactions are not statistically significant. Two types of responses can be described, based on the latency variations. Figures 1 and 2 show good examples of the so-called “short latency type” of targeting reflexes, characterized by a latency of the ipsilateral auricular component of \( \leq 50 \) ms and of \( \leq 150 \) ms for oculo-cephalic responses. 62% of the unconditioned targeting reflexes belong to this “short latency type”. Responses of the “long latency type” with latencies between 150 and 700 ms were not systematically studied due to their low number and their high degree of variability. However, in spite of long latent oculo-cephalic responses, short latency reactions of the ipsilateral ear could often been observed in the “long latency type” (see Fig. 8).

In some experimental sessions the intensity of the auditory stimulus

![Fig. 1. Unconditioned targeting reflex after auditory stimulation from anterior-right direction. T, tone stimulus, 1, right EOG, 2, right auricular EMG, 3, left auricular EMG, 4, EMG of the neck.](image-url)

![Fig. 2. Unconditioned targeting reflex after auditory stimulation from posterior-left direction. Denotations as in Fig. 1.](image-url)
was suddenly increased (>100 dB). In such a case the latency of all components became very short — around 20 ms — and the targeting reflex was preceded by a startle reaction (Figs. 3 and 4). In strong contrast to the majority of the short latent ipsilateral auricular reactions, the ear contralateral to the sound source is involved more irregularly and it sometimes does not show any response at all. Figure 5 shows the three components after successive auditory stimulation — anterior right and anterior left. In both cases short latency reactions of the ipsilateral ears are observed, but no contralateral activation of the EMG is found.

![Graph showing mixed startle-targeting reaction](image1)

Fig. 3. Mixed startle-targeting reaction. Denotations as in Fig. 1.

![Graph showing startle reaction and delayed targeting reflex](image2)

Fig. 4. Startle reaction and delayed targeting reflex. Denotations as in Fig. 1.

*Elaboration of conditioned targeting reflexes.* About 90% of the conditioned responses belong to the “short latency type” described above. Besides, during the elaboration of the conditioned instrumental reaction the inter and intraindividual variability of the response pattern decreases remarkably, but the sequence of latencies of the three compo-
nents is maintained (Fig. 6 and Table II). The latencies of the auricular reaction differed from those of the oculo and cephalic reactions ($p < 0.05$, Walsh-test). But the latencies of the ocular and cephalic reactions did not differ significantly among themselves. The conditioning process decreases the variability of latencies of the components and has a stabilizing influence on the reflex. In all the studied animals the latency and duration of the recorded motor components tended to become very similar in the consolidation stage of the conditioning process (Fig. 7).

Fig. 5. Unconditioned audio-visual targeting reflex after auditory stimulation from anterior-right (a) and anterior left direction (b). Denotations as in Fig. 1.

Fig. 6. Mean latencies of the auricular (crosses) and ocular (closed circles) responses in different stages of development of the targeting reflex. I, unconditioned reflex, II, formation of the conditioned reflex, III, consolidation of the conditioned reflex. Values represent mean reactions of 5 cats during 5 sessions.
Latencies of the motor components of the unconditioned and conditioned audio-visual targeting reflex. Values represent means from reactions of 5 cats during 5 sessions

<table>
<thead>
<tr>
<th>Targeting reflex</th>
<th>Latencies (ms)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ear</td>
<td>eye</td>
<td>head</td>
</tr>
<tr>
<td>Unconditioned</td>
<td>78±49</td>
<td>162±42</td>
<td>129±51</td>
</tr>
<tr>
<td>Conditioned</td>
<td>29±7</td>
<td>84±18</td>
<td>71±9</td>
</tr>
</tbody>
</table>

Differences between unconditioned and conditioned targeting reflexes are statistically significant (p < 0.05, Walsh-test).

This fact contrasts with the interindividual variability observed in the unconditioned situation.

The influence of the direction of the sound on the latency and duration of the auricular reaction can be observed in a concrete example in Table III. Here there are also remarkable response latency differences of ipsi and contralateral auricular reactions, depending on whether the response is elicited by sources placed within or outside the animal’s visual field.

Habituation of the unconditioned targeting reflex. When the animals were stimulated in successive trials by the standard tone, in most cases

![Fig. 7. Typical auricular and ocular responses of the five cats (a–e) after auditory stimulation from the right direction at the end of the conditioning. 1, right EOG, 2, right auricular EMG.](image)

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Mean latency and duration of the right auricular EMG of cat 3 at the end of the conditioning, when the animal was stimulated by sound from different directions. Values represent means from 30 trials.

<table>
<thead>
<tr>
<th>Direction of sound</th>
<th>Latency (ms)</th>
<th>Duration (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior-right</td>
<td>21±10</td>
<td>324±250</td>
</tr>
<tr>
<td>Anterior-left</td>
<td>39±25</td>
<td>225±153</td>
</tr>
<tr>
<td>Posterior-right</td>
<td>27±13</td>
<td>1121±667</td>
</tr>
<tr>
<td>Posterior-left</td>
<td>137±201</td>
<td>100±180</td>
</tr>
</tbody>
</table>

A very rapid habituation could be observed. Figure 8 shows the inhibition of the four motor components in a cat, when the animal was confronted with the experimental situation for the first time. The first acoustic trial (Fig. 8a) elicits a distinct reaction of all the recorded components. After the first repetition of the stimulus (Fig. 8b) the oculocephalic response is abolished and only the ipsi and contralateral auricular reaction can be observed. Then the duration of these response patterns is strongly diminished (Fig. 8c) and they are finally also extinguished (Fig. 8d).

The mean numbers of auricular, ocular and cephalic responses for

![Fig. 8. Habituation of the unconditioned audio-visual targeting reflex after repeated auditory stimulation (a–d) from the right direction. Denotations as in Fig. 1.](image-url)
5 cats tested during 5 sessions are plotted in Fig. 9. The curves demonstrate the rapid but different habituation of the three motor components.

After habituation on successive trials within a session the acoustic parameters were changed to elicit further responses. The mean numbers of the auricular, ocular and cephalic responses in the intra and inter-session habituation are shown in Table IV.

Each of the three differences between the mean values of the motor components is statistically significant ($p < 0.05$, Walsh-test). If we compare the mean number of each type of responses on successive sessions, the inhibition of the ocular, auricular and cephalic reactions is also clearly differentiated (Fig. 10).

![Fig. 9. Intrasession habituation of the auricular (crosses), ocular (closed circles) and cephalic (open circles) responses. Values represent mean percentage of responses of 5 cats during 5 sessions.](image)

**TABLE IV**

The percentage of the auricular, ocular and cephalic responses of individual cats. Values represent mean percentage of responses during 5 sessions and 50 trials for each animal

<table>
<thead>
<tr>
<th>Cat</th>
<th>Percentage of responses</th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Ear</td>
<td>Ocular</td>
<td>Cephalic</td>
</tr>
<tr>
<td>C1</td>
<td>52±13</td>
<td>39±9</td>
<td>18±6</td>
</tr>
<tr>
<td>C2</td>
<td>81±14</td>
<td>56±28</td>
<td>25±11</td>
</tr>
<tr>
<td>C3</td>
<td>54±21</td>
<td>38±15</td>
<td>29±12</td>
</tr>
<tr>
<td>C4</td>
<td>73±16</td>
<td>47±8</td>
<td>15±11</td>
</tr>
<tr>
<td>C5</td>
<td>62±19</td>
<td>35±23</td>
<td>13±7</td>
</tr>
</tbody>
</table>

Mean of the group | 64±11* | 43±8* | 20±6* |

* The differences between the values are statistically significant ($p < 0.05$, Walsh test).
Acute extinction of the conditioned targeting reflex. The extinction process of the conditioned alimentary reaction, i.e., repeated activation of the loudspeaker without food presentation, is characterized by a very high resistance to inhibition compared with the habituation of the unconditioned response. The sequence of inhibition — head — eye — ear —

Fig. 10. Intersession habituation of the auricular (crosses), ocular (closed circles) and cephalic (open circles) responses. Values represent mean percentage of responses of 5 cats.

Fig. 11. Extinction of the conditioned targeting reflex after repeated stimulation from the left side without reinforcement. a, 1st stimulus, b, 10th stimulus, c, 20th stimulus, d, 40th stimulus, e, 60th stimulus, f, 90th stimulus, g, 115th stimulus, 1, right EOG, 2, left auricular EMG.
remains the same as in the habituation of the unconditioned response.

The unconditioned reaction needed only a few repetitions of the stimulus to become completely inhibited. The conditioned reaction, on the contrary, needs more than a hundred stimulations without reinforcement before the auricular component is fully inhibited (Figs. 11 and 12).

The following sequence could be observed in the extinction process of the conditioned response:

Stimulation 1–10: The reaction configurates a clear and exact head movement to reach the visual fixation of the source of sound. There is no difference in latencies compared with consolidation stage in the training process.

Stimulation 11–50: The head movements often appear, but only a smaller angle is involved. The ocular component occurs regularly, but its mean latency is increased.

Stimulation 51–100: There are only cursory head movements, the ocular component becomes irregular, latency and variation of the ocular component are strongly increased.

More than 100 stimulations: The auricular component begins to get extinguished, but it is still possible to observe some well known short latency ear movements.

This pattern of extinction is observed in all animals, but the number of extinction trials depends on the experimental conditions and on the individual (motivational) state of the animal.
DISCUSSION

The main results of the present study can be summarized as follows: the unconditioned and conditioned audio-visual targeting reflex begins with movements of the pinna followed by oculo-cephalic reactions; the ipsilateral pinna movements are the most constant reactions; the unconditioned targeting reflexes are characterized by a rapid and sequential habituation of the three components; during the build-up of a conditioned audio-visual targeting reflex, the mean latencies of each of the three components reach their lowest values in the consolidation stage of the training process; the auricular component ipsilateral to the sound source is the one most resistant to extinction.

The audio-visual reflex can be considered as an intersegmentary reflex involving ears, eyes, head and postural adjustments in such a way that one effector component is able to trigger the following components of the reflex (1, 22, 27).

One of the most important properties of the unconditioned audio-visual targeting reflex is its rapid habituation. The habituation has been studied by different authors (1, 6, 7, 21, 29) and it seems to be the main factor involved in the high variability of the effector pattern of the targeting reflex. Thompson and Masterton (28) have tried to minimize the rate of habituation of the head movements to the tone source by testing the cats irregularly with an average of one session in three days and with two to five sound presentations in one session. They observed that the latencies of the cephalic responses ranged between 20 and 80 ms. In relation to our measurements of the oculo-cephalic components, these latencies are rather small. However, they fit reasonably well with latencies for startle reactions and some targeting reactions of the "short latency type" described here. The contradiction is probably based on the different recording systems. The latencies in the present work were measured by miographic recording, while Thompson and Masterton used a device sensitive to movements of the head and it is possible that they may have also recorded startle and ear movements at the initiation of the cephalic displacement. Besides habituation, ear movements may be modulated by the oculo-auricular reflex (12) and other co-innervations of the M. retroauricularis (13, 14).

The auricular reaction seems to play an important role in the integration of the audio-visual targeting behavior of the cat. This fact has been studied by Siegmund and Santibáñez-H. (27) in cats and by Schneider and Möhres (25) in bats. Their works indicated that the denervation of the external ear muscles determined a drastic reduction of the ability of the animals to localize the source of sound. The de-
nervated animals tried to counterbalance the deficit by a compensatory movement of the head without reaching the same level of accuracy as the normals.

The ear ipsilateral to the source of tone presented the most stable pattern of movement and the shortest latency of all the other components of the targeting reaction. This fact suggests that both auricular effects are not rigidly coupled. The ipsilateral ear movement seems to be more important than the contralateral one. In fact, Siegmund and Santibáñez-H. (27) have shown that the unilateral denervation of the ear causes a stronger deterioration of localization accuracy towards the ipsilateral sources than to the contralateral ones.

The cephalic responses appear significantly later than the auricular responses and are extremely variable when compared to the auricular component. The sequence of the eye and head movements is not a simple question. Sporadic observations have shown that in the very first stages of the conditioned targeting reactions, the eyes move along the head, but once the animal is familiar with the configuration of the experimental arrangement, the head can start moving together with or even before the eyes. It is perhaps necessary to perform more experimental work in order to clarify this situation. However, on the one hand cephalic and pinna movements are complementary in modifying the auditory informational input, especially regarding the binaural time interval and frequency-intensity cues. On the other hand, head movements are important in the visual part of the reflex: in the coordination of eye-head movements necessary for the organization of the gazing behavior. In cats almost all saccades of amplitude larger than 4° are accompanied by head rotation (3). The timing between the onset of a saccade and that of the head movement is extremely variable. Commonly the eye leads this process and the head responds 20–50 ms after the beginning of the ocular movements (2, 3, 9). It is possible to postulate that in a pure auditory localization process the head may lead the process and the eyes can follow after the cephalic start. That could be an explanation for the unusual pattern of eye-head coordination with negative head lag observed by Harris (9).

The difference in latency of the auricular and oculo-cephalic response presents the problem of the pathways responsible for both types of reactions. In cats the shortest latencies of the pinna reflex are within the time range of the intra-aural reflexes (4) and other facial defensive responses, such as eye-blink reflex (18, 19). This short latency suggests that the first integrative level of this complicated reflex occurs in the brainstem (10, 20), and can eventually be mediated by the superior olivary complex and the dorsomedial part of the facial nucleus. In our
laboratory, Giavelli (8, 23) demonstrated, that neurons of the medial nuclei of the superior olivary complex are able to integrate binocular, contralateral facial and bilateral somesthetic information from the forelimbs, besides the well known binaural inputs. Siegmund (23, 26) found responses to clicks, flashes and to electrical stimulation of the pinna in the facial nucleus, especially in the part of the nucleus which provides motor supply to the external ear muscles. The shortest latencies towards acoustic stimuli were found to be around 5 ms. Furthermore there are some morphological evidences for direct ipsi and contralateral connections going from the superior olivary complex to the dorsomedial part of the facial nucleus (15, 16).

The most important neuronal level involved in the neural integration of the auricular and oculo-cephalic reactions seems to be the superior colliculus. Several proofs support the assumption that the superior colliculus is involved in the initiation of the eye-head gaze changes (3, 9) and in the control of pinna movements (5, 11, 24). The superior colliculus seems to integrate different modalities of information, besides producing motor outputs which configure postural patterns, in this way optimizing both inputs as well as the best posture to respond.

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